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Neural correlates of shape-color binding in visual working memory

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Abstract

The present study addressed an outstanding issue regarding feature binding in working memory (WM): Whether this function engages specific resources relative to those required to process individual features. We investigated the brain regions supporting the encoding and maintenance of features and bindings in a change detection task, in which 22 healthy young volunteers remembered visual arrays of abstract shapes, colors or shape-color bindings while undergoing fMRI. After an unfilled delay they saw a second array and judged whether the features or combination of features presented across the two arrays were the same or different. Temporary retention of feature bindings was found to involve additional cortical regions compared with retaining single features, regardless of whether the number of objects or the number of features differed between feature-only and binding conditions. This binding-specific activation is consistent with the involvement of different neural generators that collectively support visual temporary memory for features and for feature bindings. Regions within the parietal, temporal and occipital cortex, but not within the prefrontal cortex or the medial temporal lobe, appear to support the integrated object binding function investigated in this study. Our findings suggest that both individual features and their binding within integrated objects are used to represent complex objects in WM.

Key Words: Working Memory Binding; Feature Integration; Conjunctive Representations; Unitization; fMRI

Highlights

- (1) Temporary memory for single and bound features relies on different brain regions.
- (2) These brain resources dissociate during the maintenance phase.
- (3) The maintenance of bound information may limit WM capacity.
- (4) Posterior cortical regions may support feature binding in WM.

1. Introduction

Many daily tasks require us to hold visual information temporarily in mind, preserving combinations of features such as colored shapes. Two central questions regarding these functions of visual working memory (VWM)¹ concern the limits on its capacity to process and store multi-feature objects, and the cognitive resources required to process and store them relative to single-feature objects. Neuroimaging studies have mainly focused on the former question (Shafritz, Gore, & Marois, 2002; Todd & Marois, 2004; 2005; Xu, 2007; Xu & Chun, 2006) and behavioral studies on the latter (Allen, Baddeley, & Hitch, 2006; Allen, Hitch, & Baddeley, 2009; Allen, Hitch, Mate, & Baddeley, 2012; Brockmole & Logie, 2013; Karlsen, Allen, Baddeley, & Hitch, 2010; Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001). The present fMRI study focused on the second question, investigating whether holding features bound within integrated objects in VWM (i.e., shape and color) engages additional neural resources compared to the maintenance of single features.

Feature binding in VWM has been commonly investigated using change detection tasks which assess memory by comparing the content of an initial array of items with a second array presented after a short retention interval (Allen et al., 2006; 2009; 2012; Alvarez & Cavanagh, 2004; Baddeley, Allen, & Hitch, 2011; Gajewski & Brockmole, 2006; Logie, Brockmole, & Vandenbroucke, 2009; Olson & Jiang, 2002; Wheeler & Treisman, 2002; Xu, 2002). Contrasting memory for arrays of single visual features (e.g. a set of shapes) with memory for arrays of the same number of objects comprising multiple features (e.g. a set of colored shapes) has enabled the investigation of whether binding features within integrated

¹ In the literature on visual attention, visual perception, and feature binding, the terms 'visual short-term memory' and 'visual working memory' tend to be used interchangeably. We view visual short-term memory as comprising a temporary store that is one of a range of functions of visual working memory, which in turn is a set of functions within a broader, multi-component working memory, and we use the terms in this way throughout the manuscript. This issue is outside the scope of the present paper and the adopted term 'visual working memory' (VWM) is intended to be theoretically neutral here with respect to models of working memory. See Logie (2011) and Logie and Niven (2012) for reviews and detailed discussion.

objects in VWM requires dedicated resources. Some studies have reported no differences in memory performance between these two tasks (e.g., Brockmole, Parra, Della Sala, & Logie, 2008; Gajewski & Brockmole, 2006; Luck & Vogel, 1997; Vogel et al., 2001) while others have reported evidence that temporary memory for bound multi-feature objects is a more demanding task than temporary memory for the same number of single-feature objects (see Olson & Jiang, 2002; Wheeler & Treisman, 2002).

These varied findings may reflect the engagement of different resources to processes feature bindings in VWM, according to the type of bound information (e.g., same or different types of features), as well as the number of objects that have to be remembered (e.g., Alvarez & Cavanagh, 2004; Brady, Konkle, & Alvarez, 2011), and whether or not object location is one of the features to be included in the binding (e.g., Delogu, Nijboer, & Postma, 2012; Hollingworth & Rasmussen, 2010; Logie, Brockmole, & Jaswal, 2011; Sapkota, Pardhan, & van der Linde, 2011; Treisman & Zhang, 2006; see also Shafritz et al., 2002). These proposals are consistent with neuroimaging findings which seem to implicate specific processes in processing bindings between visual features in VWM when these involve object location. This has been found to engage the hippocampus and prefrontal cortical regions not involved in processing the individual features (Piekema, Kessels, Mars, Petersson, & Fernandez, 2006; Piekema, Rijpkema, Fernandez, & Kessels, 2010; Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000; Sala & Courtney, 2007; Todd & Marois, 2004). Conversely, temporarily maintaining in memory bindings involving conjunctions of surface features (e.g. color-shape with location as an uninformative feature) does not appear to involve regions other than those involved in processing single features in VWM (Shafritz et al., 2002; Song & Jiang, 2006; Xu, 2007; Xu & Chun, 2007). Therefore, the type of information that is bound within complex stimuli seems to impact both on whether there are behavioral costs of binding and on the neural resources engaged.

Nevertheless, the question of whether processing multi-feature objects in VWM engages specific resources not engaged when processing single-feature objects remains open. A handful of neuroimaging studies have investigated the neural underpinnings of capacity of VWM (Shafritz et al., 2002; Song & Jiang, 2006; Xu, 2007; Xu & Chun, 2006; 2007), but few have addressed the issue of binding-specificity by directly comparing activity associated with temporary retention of feature conjunctions with activity associated with retention of features (Shafritz et al., 2002; Xu & Chun, 2006; 2007). Shafritz et al. (2002) used a region of interest (ROI) approach to show activity related to conjunction binding within superior parietal and intraparietal regions engaged in spatial attention, but not in a sequential presentation condition in which location was uninformative. In a task in which location was again an informative feature, Xu & Chun (2006) showed load-related activity in superior intraparietal sulcus (IPS) and lateral occipital complex (LOC) for features only, and load-related activity in inferior IPS for both features and conjunctions, but no binding-specific responses in these ROIs.

These findings do not provide a clear answer to the question of binding-specificity for several reasons. First, these neuroimaging studies have investigated binding-specific and feature-related activity in conditions where irrelevant as well as relevant features have been present in to-be-remembered objects (Shafritz et al., 2002; Song & Jiang, 2006; Xu, 2007). There is evidence that participants may use irrelevant features as memory cues, leading them to represent bound object information in conditions aimed at assessing VWM for single features (Luria & Vogel, 2011; Marshall & Bays, 2013). Second, in order to assess the resources involved in binding surface features within integrated objects, the location of the stimuli cannot be an informative feature, for the reasons already noted (see for example Todd & Marois, 2004). Third, it is unclear whether dedicated neural resources are necessary to encode or to maintain in VWM single features or feature bindings as earlier studies have not

modeled these two memory processes separately to disentangle such contributions. Finally, because the earlier studies employed an ROI approach, little is known about the role of regions outside IPS and LOC.

The present study therefore investigated whether activity would differ for VWM encoding and maintenance of single features and feature bindings when (1) each feature dimension has to be accessed individually (i.e., single features) or concurrently (i.e., bindings), (2) location information cannot be used as a memory cue, (3) the activity corresponding to the encoding and maintenance phases can be modeled separately and (4) a whole brain rather than a region of interest approach is implemented. We also used two feature binding conditions with different set sizes, enabling tests for binding-specific activity common to these two conditions, and therefore distinct from activity reflecting an increase in feature load. If processing feature bindings in VWM requires neural resources other than those involved in the processing of individual features, these should be revealed with this approach.

2. Methods

2.1 Participants

Twenty two undergraduate students (ten males) took part in this experiment and were paid for their time. All but one were right handed. Their age range was 18-28 years ($M = 21.8$, $SD = 2.15$) and their education range was 13-20 years ($M = 16.41$, $SD = 1.65$). All reported good health and had normal or corrected to normal vision. None had color vision problems as assessed by the Color Blindness test (Dvorine, 1963). The study was approved by the UK National Health Service Local Research Ethical Committee. All participants gave written

consent prior to participation and were familiarized with the fMRI environment in a MRI scanner simulator prior to testing.

2.2 VWM binding task

The VWM task was based on a change detection paradigm previously employed in behavioral experiments (Brockmole et al., 2008; Parra et al., 2010).

Insert Fig 1 about here

The VWM task involved presenting visual arrays of four shapes or four colors, or two or four colored shapes, and was controlled by a laptop personal computer synchronized with the fMRI scanner. Stimuli for each array were randomly selected from one set of eight shapes and from one set of eight colors (see Parra et al., 2010 for a more detailed description of these stimuli). Figure 1 shows the task design. At the beginning of each trial a warning screen informed the participant as to which condition was to be tested. This was followed by a fixation period during which a white fixation cross changed to black to indicate that the study array was about to be displayed. The study array was then presented for 500 msec. This was followed by a blank display with a gray background for an unfilled delay period of a variable duration. The delays were randomly and evenly selected from a set of 4 (see Figure 1 and Methods for a description of the temporal design optimization). The test display was presented after the delay and remained on for 2000 msec. After the test display an inter-trial interval (ITI) of variable duration was presented. On 50% of trials, the study and test displays presented identical items. On the other 50%, there were changes between the study and test

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displays. Participants were asked to detect when a change had occurred and to respond whether the two displays showed the ‘same’ or ‘different’ items by pressing one or other of two previously assigned buttons with their preferred hand. Items randomly changed locations from study to test. This rendered location an uninformative feature, so location could not be used as a memory cue. All study-test delays also exceeded the duration at which a random change in location has been found to affect performance in detection of changes to color and shape (Logie et al., 2011).

The VWM task consisted of four conditions. Two conditions assessed VWM for single features and two assessed the binding of these features in visual VWM. In the Shape Only and Color Only conditions the study arrays consisted of black shapes or colors (Figure 1). In the test array for the different trials, two shapes or colors from the study array were replaced by new shapes or new colors. In the Shape-Color Binding conditions the arrays consisted of combinations of shape and color. In the test array for different trials two shapes swapped the colors in which they had been shown in the study array. Hence, memory for bindings of shape and color in the study display was required in order to detect this change. In none of the three conditions were features repeated within a given array. For each condition there were 10 practice trials followed by 32 test trials. Trials were fully randomized across participants and conditions were blocked and delivered in a counterbalanced order.

2.3 Experimental procedures

Pre-scanning session: the participants entered a scanner simulator to familiarize themselves with the fMRI environment, and to check for any potential difficulties (e.g., claustrophobia). Their color vision was assessed and the informed consent signed.

Scanning session: outside the scanner the participants underwent a short practice session in which they performed 10 trials for each condition of the VWM binding task. They then entered the fMRI scanner and performed two 20 min blocks of 48 trials each.

2.4 fMRI design optimization

The temporal characteristics of the task were determined in order to ensure adequate efficiency of the design for the key fMRI contrasts, whilst manipulating condition between blocks as in previous behavioral studies). Custom scripts in MATLAB (The MathWorks, Natick, MA, USA, <http://www.mathworks.com/>) were used to estimate the efficiency of encoding and maintenance phase between-condition contrasts in order to select the best trial parameters. Delay periods of 2, 4, 6 and 8 sec and inter-trial intervals of 4, 8, 12, 16 sec were equally distributed across the 32 trials in each condition, and presented in random order. Collinearity between the maintenance phase regressors and those for the encoding and probe periods of the task was approximately 0.5. The fMRI analysis assessed activity uniquely predicted by the encoding and maintenance trial regressors, i.e., specifically attributable to the encoding and maintenance phases (Curtis & D'Esposito, 2003; Sakai, Rowe, & Passingham, 2002; Zarahn, Aguirre, & D'Esposito, 2000).

2.5 fMRI image acquisition

Imaging was carried out at the University of Edinburgh Brain Research Imaging Centre (BRIC; <http://www.sbirc.ed.ac.uk/>) on a 1.5 T GE Sigma MRI scanner (GE Medical, Milwaukee, USA). After a localization scan, a structural T1 weighted sequence was acquired (5 contiguous 5 mm coronal slices; matrix = 256 x 160; fov = 24 cm; flip angle 8°). During the VWM task, contiguous interleaved axial gradient-echo planar images (EPI) were acquired parallel to the intercommissural plane in two continuous runs (TR/TE = 2000/40ms; matrix =

64 x 64; field of view = 24 cm; 27 slices per volume, thickness = 3.5 mm, 1.5 mm gap). Each acquisition consisted of 598 volumes, of which the first three volumes were discarded to allow for T1 equilibration effects. Following this, a T2-weighted fast spin-echo sequence was also obtained.

2.6 Data analysis

2.6.1 Behavioral

The proportion of correct recognition responses (hits and correct rejections) was calculated. This variable was subjected to repeated-measures ANOVA with the factor condition [Shape Only vs. Color Only vs. Binding 2 vs. Binding 4].

2.6.2 fMRI

2.6.2.1 Preprocessing

Preprocessing and statistical analysis were conducted using SPM8 (updates 4010 and 4290, respectively) (Statistical Parametric Mapping: The Wellcome Department of Cognitive Neurology and collaborators, Institute of Neurology, London, UK, <http://www.fil.ion.ucl.ac.uk/spm/>) running in MATLAB 7.7.0471 (The MathWorks, Natick, MA, USA, <http://www.mathworks.com/>). To assess data quality, reconstructed images were examined for problem scans by outlier detection (variance of > 5 standard deviations; see Morcom et al., 2010). If identified, problem scans were replaced by the average of the previous and subsequent scans, and modeled as confounds in the design matrix with a “1” at the appropriate timepoint in a column of zeros (for design details see below). Problem scans comprised 0.31% of the total. All images were corrected for differences in slice acquisition using temporal sinc interpolation to match the middle slice in time, and then realigned spatially to the first volume of each run using B-spline interpolation. Following co-

registration with the mean EPI image, each participant's T1 structural scan was segmented using extended prior probability maps (SPM8; Ashburner & Friston, 2005). Segmented T1 images were then normalized to the standard anatomical space of the Montreal Neurological Institute (MNI), using segmentation parameters and DARTEL diffeomorphic mapping functions (Ashburner, 2007; Ashburner & Friston, 2009). Finally, the same mappings were applied to the functional time series to bring it into the standard space.

2.6.2.2 *Statistical modeling*

A two-level General Linear Model (GLM) summary statistical procedure was employed (Penny & Friston, 2004). At the individual participant level, the GLM incorporated both sessions, with a constant term for each. For each session, the experimental conditions were modeled using separate covariates for the encoding, maintenance and probe trial phases. Trials attracting correct responses for the first three conditions (Shape Only, Color Only, Shape-Color Binding 2) each generated 3 covariates (e.g., Shape-ENCODING, Shape-MAINTENANCE, Shape-PROBE). For the fourth condition (Shape-Color Binding 4), correct trials and error trials were modeled separately with 3 covariates each. Trials in the first 3 conditions attracting incorrect responses were then collapsed to provide another 3 covariates for the 3 trial phases. The covariates in the GLM comprised sequences of delta functions at the event onset times for each condition and trial phase, convolved with a canonical hemodynamic response function (HRF; Friston et al., 1998), downsampled at the midpoint of each scan. Modeled event durations were 0.5 sec for the encoding phase (i.e., the duration of stimulus presentation) and 2 sec for the probe phase (i.e., the duration of probe presentation). The variable maintenance phase delay durations across trials (2, 4, 6 and 8 sec), included for design optimization purposes (see 2.4), were also modeled. Therefore, the maintenance period covariate for each experimental condition included trials with varying

delays. Six covariates, representing the 3 rigid body translations and rotations estimated in the realignment stage, were included for each session to capture residual movement-related artifacts. Any problem scans were also modeled using separate covariates (see Methods > Data analysis > fMRI > Preprocessing). Voxel-wise parameter estimates for each covariate were obtained using Restricted Maximum Likelihood (ReML), modeling autocorrelation across scans with an AR(1) plus white noise model (Friston et al., 2002). The data for each session were highpass filtered to 1/128 Hz and scaled to a grand mean of 100 across all voxels and scans within a session.

Linear contrasts of the first-level parameter estimates were the data for the second-level analyses, which treated participants as a random effect. Details of group-level models and contrasts are given in the Results (fMRI findings: Data Analysis Strategy). ANOVA models were implemented in SPM8's Flexible Factorial utility (see Results: Analysis Strategy). The family-wise error (FWE) rate was corrected at a whole-brain level. Statistical parametric maps (SPMs) were initially thresholded at $P < 0.001$, uncorrected. To control the FWE rate at $P < 0.05$, an additional cluster extent threshold of 66 contiguous voxels was then applied, determined using the AlphaSim Monte Carlo simulation tool from AFNI (Analysis for Functional NeuroImaging; <http://afni.nimh.nih.gov/>) (Cox, 1996). For inclusive masking of contrasts, masks were applied at an uncorrected threshold of $P < 0.001$, and the final masked image was thresholded at the FWE-corrected level. For exclusive masking, i.e., to discount voxels showing any hint of an exclusively masked effect, masks were applied at an uncorrected threshold of $P < 0.05$. Locations of the peaks of suprathreshold clusters were established with reference to participants' mean EPI and structural images, and the MNI reference brain (Cocosco, Kollokian, Kwan, & Evans, 1997). They were then labeled using the systems of Talairach and Tournoux (Talairach & Tournoux, 1988) and Brodmann (Brodmann, 1909). For the *a priori* ROI analyses, we employed a small volume correction

based on Gaussian Random Field theory, using spheres of radius = 5 mm around coordinates of interest (see Results: Data Analysis Strategy and *Supplementary Material*; Worsley et al., 1996).

Insert Table 1 about here

3. Results

3.1 Behavioral data analysis

Figure 2 shows mean performance data for the four conditions of the VWM binding task. A repeated-measures analysis of variance (ANOVA) with the factor Condition (Shape Only vs. Color Only vs. 2 Shape-Color Binding vs. 4 Shape-Color Binding) for accuracy revealed a significant effect [$F(3,63) = 75.01$, $p < 0.001$, $\eta_p^2 = 0.88$, $\beta = 1.0$]. Bonferroni-corrected post-hoc contrasts revealed significantly better performance for Color Only than for both Shape Only [Mean difference (MD) = 0.18, $p < 0.001$] and Binding 4 [MD = 0.30, $p < 0.001$], but not than Binding 2 [MD = 0.006, n.s.]. Performance for the Binding 2 condition was better than for the Shape Only Condition [MD = 0.18, $p < 0.001$] and the Binding 4 condition [MD = 0.29, $p < 0.001$]. Binding 4 performance was also significantly lower than for both Shape Only [MD = 0.12, $p = 0.001$] and Binding 2 [MD = 0.29, $p < 0.001$].

Insert Fig 2 about here

3.2 *fMRI data analysis strategy*

The main, whole-brain fMRI data analysis focused on (a) binding-specific activity and (b) feature-related activity, for the encoding and the maintenance trial phases. For each participant and phase, group analysis employed 4 basic *T*-contrasts which evaluated the simple effects of activity elicited by each condition versus fixation, for trial attracting correct responses only. These contrasts were therefore Shape Only, Color Only, Binding 2 and Binding 4, for the encoding and the maintenance phases.

The group-level analyses for each trial phase were implemented in repeated-measures ANOVA models with 4 levels, comprising the 4 basic contrasts. For both encoding and maintenance phases, analyses were carried out within a search volume restricted to regions which showed (i) substantial responses during one or more conditions in that trial phase with respect to the fixation inter-trial baseline (defined using an *F*-test at an uncorrected threshold of $P < 0.001$), and (ii) average activity increases during VWM encoding and maintenance relative to the fixation inter-trial baseline for that trial phase (defined using a *T*-test at an uncorrected threshold of $P < 0.05$). Details of the resulting search volumes for the encoding and maintenance phases are given along with a schematic of the procedure in *Supplementary Material (Supplementary Figure 1)*. Within the relevant search volume for each trial phase, results were thresholded at a whole-brain FWE-corrected level of $P < 0.05$ for the purposes of statistical inference (see Methods). This procedure made the inference slightly more conservative than it would have been using a whole-brain search volume, but ensured that

results would be readily interpretable in terms of activity increases against the inter-trial baseline.

Our main hypothesis was that processing multi-feature objects in VWM requires additional resources not required to process the constituent features. We tested for binding-specific activity using a unidirectional (T) contrast to determine which regions within the search volume showed an activity increase common to the two binding conditions relative to the two feature conditions (Binding 2 AND Binding 4 versus Shape Only AND Color Only). To discount those regions also showing differential activity in the binding conditions according to set size, we exclusively masked the resulting SPM with the bidirectional (F) contrast Binding 2 versus Binding 4 (see Methods, Statistical modeling for masking procedures). Regions showing differential activity between the two feature conditions were discounted by exclusive masking with the bidirectional (F) contrast of Shape versus Color.

Feature-related activity was investigated by contrasting the two feature conditions (Shape Only versus Color Only) using a bidirectional (F) contrast. To discount those regions also showing any binding-specific activity, we exclusively masked the resulting SPM with two contrasts comparing activity in each feature condition with that in the binding conditions (Shape Only (OR Color Only) versus Binding-2 AND Binding-4). *Post hoc* contrasts were used to determine the direction of any significant effects (Color > Shape, or Shape > Color), and to test simple effects of each condition against fixation (see Methods, and Tables 2 and 3).

We were also interested in investigating whether the regions showing binding-specific activity would overlap with regions reported in previous studies. A set of ROI analyses were conducted using coordinates defined *a priori* from these studies, details of which are given in the *Supplementary Material (Supplementary Table 1)*.

3.3 Encoding phase

Binding-specific activity. The whole-brain analysis of binding-specific activity did not reveal any suprathreshold clusters for the encoding phase, although the *a priori* ROI analyses revealed significant activity in right fusiform in the vicinity of the LOC (BA37; peak: $x = 45$, $y = -63$, $z = -15$; see *Supplementary Material*, see also Song & Jiang, 2006).

Feature-related activity. Regions showing significant differences in encoding phase activity between the two feature conditions are illustrated in Figure 3A and Table 1.

Insert Fig 3A and B about here

Insert Table 1 about here

Post-hoc tests revealed that the middle frontal, inferior temporal, postcentral and fusiform gyrus regions showed activity increases for shape relative to color encoding, while those in precentral gyrus, medial frontal gyrus and thalamus showed activity increases for color relative to shape encoding.

3.4 Maintenance

Binding-specific activity. The analysis of binding-specific activity during VWM maintenance revealed a set of suprathreshold regions including clusters in fusiform, postcentral and middle frontal gyri as well as in the inferior parietal lobule. These are shown in Table 2 and Figure 3B. Of note, this pattern of findings did not differ when regions also showing differences between Binding 2 and Binding 4 were included rather than discounted (see *Supplementary Figure 2*).

Post-hoc tests were also carried out to characterize the apparent overlap between the regions showing feature-related encoding activity and those showing binding-specific maintenance activity. These tested for feature-related encoding activity within 5 mm radius spheres centered around peak coordinates of regions showing binding-specific maintenance activity, using small volume correction ($P < .05$, FWE corrected; see Methods). These confirmed that activity overlapped in the vicinity of the left LOC (BA37; peak: $x = -46$; $y = -56$; $z = -16$; see Table 1 and Figure 3). There was also reliable binding-specific maintenance activity analysis in the nearby left LOC ROI defined from Song and Jiang's (2006) results (BA37; $x = -48$; $y = -60$; $z = -21$; see *Supplementary Material*).

Insert Table 2 about here

Feature-related activity. The analysis of feature-related activity during the VWM Maintenance phase revealed a set of suprathreshold regions including clusters in left inferior frontal gyrus and right anterior cingulate gyrus. These are shown in Table 2 and Figure 3B.

Post-hoc tests revealed that these regions were engaged to a greater degree in maintaining colors than shapes.

4. Discussion

The present fMRI study investigated whether processing the bindings of shapes and colors in VWM requires neural resources other than those involved in processing shape and color only. The fMRI design enabled us to examine the brain networks specifically engaged during the encoding and maintenance of single features or integrated objects in VWM. Our principal findings were: (1) binding-specific activity was observed during maintenance as well as during encoding, and engaged regions within the ventral visual stream and lateral parietal cortex, and (2) the binding-specific activity during maintenance did not differ according to whether 2 or 4 bound objects were retained. Feature-related activity was observed during both encoding and maintenance phases.

4.1.1 *Behavioral findings*

The behavioral data showed that holding 2 bindings in VWM was an easier task than holding 4 bindings. Performance with 4 shapes fell between performance with 2 bindings (highest) and performance with 4 bindings (lowest), thus suggesting that when the number of to-be-remembered objects was the same across the binding and the shape only conditions (set size 4), binding incurred a cost behaviorally. Behavioral findings have varied in this regard (e.g., Brockmole et al., 2008), but it does not follow that engaging an additional resource will always be reflected in behavioral performance (e.g., Allen et al., 2006; see Logie, 2011). However, our fMRI data speak directly to this issue and support the proposal of a specific binding process or processes that recruit additional resources.

4.1.2 *Encoding features and bindings in VWM*

No binding-specific activity was detected during the encoding phase in the whole-brain analysis. However, there was binding-specific activity in the right LOC ROI from Song and Jiang's (2006) study. This finding, and those from the maintenance period discussed below, suggests that different neural resources can be engaged during temporary memory for bindings compared with individual features. Encoding phase activity also differed according to whether shapes or colors were to be remembered. In line with existing evidence, encoding shapes activated regions within the ventral visual stream (i.e., right fusiform gyrus and left inferior temporal lobe) (Gerlach, Law, Gade, & Paulson, 1999; Pennick & Kana, 2012). The right fusiform region showing activity specific to shape encoding was adjacent to the right lateral fusiform LOC area showing binding-specific activity in the *a priori* ROI analysis. In Song and Jiang's (2006) study, the latter area showed equivalent activity increases for processing shapes and bindings in VWM relative to colors. Given prior data on the role of LOC in visual object recognition, the encoding phase activity here in the present study may have reflected the encoding of shape as a prerequisite for the temporary maintenance of either shape information alone or shape-color bindings, rather than the physical differences between the stimulus arrays. Both interpretations are consistent with the documented role of the LOC in visual object recognition (Grill-Spector, Kourtzi, & Kanwisher, 2001).

4.1.3 *Maintaining bindings in VWM*

Our fMRI data support the proposal of a specific binding process or processes engaged during the retention interval as well as in the encoding phase. If retaining 4 bindings required similar neural resources to those used to retain 4 shapes, there would be no binding-specific activity when these conditions are contrasted. However, as we have shown, this was not the

case (see also Xu, 2007; Xu & Chun, 2007). Regions showing suprathreshold activity during the maintenance of bound features in VWM were mainly located in the left hemisphere and included fusiform gyrus, superior and inferior parietal cortex, and dorsal premotor cortex. As noted in the Introduction, previous studies of conjunction binding in VWM, as well as studies of feature-location binding, have implicated superior parietal, posterior intraparietal and lateral occipital regions in binding (Shafritz et al., 2002; Todd & Marois, 2004; 2005; Xu, 2007; Xu & Chun, 2007). Our *a priori* ROI analyses did not reveal binding-specific activity in these parietal regions, but did find activity in a previously reported left LOC region (Song & Jiang, 2006; Xu & Chun, 2006; *Supplementary Table 1*). We also demonstrate binding-specific activity in several regions not examined in previous studies. The parietal regions showing binding-specific maintenance activity in the present study were anterior to ROIs previously examined. One region (left postcentral gyrus/superior parietal lobule, BA2/7) was more superior (Shafritz et al., 2002; Todd & Marois, 2004; 2005; Xu, 2007; Xu & Chun, 2007). The other region (left inferior parietal lobule, BA40/2) was more inferior, located in the vicinity of the supramarginal gyrus and anterior IPS.

There are several possible reasons why we did not find binding-specific activity in the parietal regions previously examined. As noted in the Introduction, in earlier studies participants have always studied multifeature objects for the feature as well as the conjunction conditions (Shafritz et al., 2002; Todd & Marois, 2004; 2005; Xu, 2007; Xu & Chun, 2007). In our study features and bindings were tested separately, the conditions assessing single feature processing presenting objects with a feature each and the conditions assessing feature binding presenting objects with two features each. Contrasts performed using these two approaches may yield different outcomes (see Marshall & Bays, 2013). We consider the design used in the current study to provide a purer measure of binding specificity, as well as yielding measures specific to the maintenance trial phase.

An important clue to how the activity we observe supports VWM binding may also lie in another difference between our tasks and those employed previously (e.g., Shafritz et al., 2002; Todd & Marois, 2004; 2005; Xu, 2007; Xu & Chun, 2007). In our study we assessed change detection using whole displays at test, whereas these earlier studies used single probes (Shafritz et al., 2002; Song & Jiang, 2006; Xu, 2007). The attentional requirements imposed by these two methods have been shown to be different, with multiple probe tasks placing a higher demand on VWM binding due to additional search processes required to match test and study items (Wheeler & Treisman, 2002; see also Cowan, Blume, & Saults, 2012; Rouder, Morey, Morey, & Cowan, 2011). The nature of this additional demand is unclear. Future studies should investigate whether it affects the way bound information is maintained or rather an effect of interference at the time of probe presentation. The parietal regions activated in our study might reflect the attention required to maintain feature representations within the ventral visual stream (i.e., fusiform gyrus, inferior temporal gyrus and lateral occipital cortex), thus binding them as unified objects. It appears that this binding-specific activity does not reflect the engagement of a limited capacity attentional system. Previous behavioral studies have observed that temporary memory for shape-color bindings is not disrupted by concurrent attentional loads any more than is temporary memory for single features (e.g. Allen et al., 2006; Gajewski & Brockmole, 2006). A key question for future studies will be how the parietal regions we identify support the parallel maintenance of bound information for multiple objects in VWM.

Interestingly, another region showing binding-specific maintenance activity outside parietal cortex (in left LOC) was also involved in shape feature encoding (see Figure 3A). This finding, as well as the encoding phase binding-specific activity in right LOC, is consistent with Song & Jiang's (2006) previous report of equivalent activity increases for their shape and binding conditions relative to their color condition in this region, given that

their binding ('both') condition assessed memory for separate features only, rather than for conjunctions, and that encoding, maintenance and probe phase activity were analyzed together. As in the earlier study, LOC activity was invariant to VWM load. Our overlapping findings in left LOC suggest that encoding features into VWM and holding these features bound together into integrated objects are functions which share resources (for a similar view (Fusser et al., 2011; Todd & Marois, 2004; Xu & Chun, 2006). We consider the implications of this finding in more detail below.

Critically, holding bindings in VWM recruits additional cortical areas relative to maintaining features, notably in the LOC and in areas of the lateral parietal cortex somewhat anterior to those implicated in conjunction binding in previous studies (see also Seymour, Karnath, & Himmelbach, 2008; Shafritz et al., 2002; Xu, 2007; Xu & Chun, 2007). The other non-parietal region involved in temporary binding maintenance was a left dorsal premotor area situated close to the superior frontal sulcus. This premotor region has been implicated in several aspects of WM all of which appear to serve general-purpose functions rather than binding-specific functions (e.g., Abe et al., 2007; Badre & D'Esposito, 2007; Badre, Hoffman, Cooney, & D'Esposito, 2009).

The regions we found to be involved in encoding and maintaining shape-color bindings in VWM are likely to reflect the type of stimuli used in our study. These regions included higher visual areas including the fusiform gyrus and the lateral occipital cortex (Staresina & Davachi, 2010). Depending on specific task requirements, different parietal regions may provide the 'glue' that keeps these features together during online processing (Shafritz et al., 2002; Song & Jiang, 2006; Xu, 2007; Xu & Chun, 2006). Our finding of no involvement of the hippocampus or other MTL structures is consistent with previous fMRI studies of intra-item bindings such as shapes and colors in VWM (Piekema et al., 2010;

Staresina & Davachi, 2010) and with neuropsychological studies (Baddeley, Allen, & Vargha-Khadem, 2010; Baddeley, Jarrold, & Vargha-Khadem, 2011).

Feature-related activity during maintenance was observed in two anterior regions; left inferior frontal gyrus and anterior cingulate. Post-hoc contrasts showed that this activity was greater during color maintenance. Considering the abstract nature (i.e., non-nameable) of the shapes presented here and the anterior distribution of this activity, it is likely that it reflects some sort of rehearsal mechanism when colors were the to-be-remembered stimuli. Although we manipulated the RGB values of these colors to render them less nameable, people may engage verbal strategies even when non-primary colors are remembered (see Henson, Burgess, & Frith, 2000; Mohr, Goebel, & Linden, 2006). This activity was not observed during the Shape Only condition suggesting that if verbal strategies were engaged, they did not support memory for the abstract polygons. Critically, the binding-specific maintenance activity was observed in different regions.

4.2.1 Behavioral ‘cost’ and binding-specificity in VWM

The encoding of information into VWM mainly reflected the features comprising the complex objects. The exception to this was the *a priori* ROI in right LOC, discussed above. Because in our paradigm stimuli differ according to the nature of the to-be-maintained information, it is not possible to draw strong conclusions about whether this encoding is automatic or reflects the instructions for maintenance of features or bindings. One possibility is that at this early stage, visual processes supported by the inferior temporal areas (i.e., inferior temporal gyrus and fusiform gyrus) may encode stimulus representations resulting from grouping processes in perception (Seymour et al., 2008).

The binding-specific maintenance period activity did not vary according to whether 2 or 4 objects were held in VWM (see Figure 3B). This is consistent with other findings that

overloading VWM does not lead to increases in brain activity: instead, this attains a plateau once capacity is reached (Xu, 2007). However, our study was not designed to investigate VWM capacity limits, which are difficult to determine in the change detection task used in our study (see for example Cowan et al., 2012 for a recent proposal about different capacity models based to be used based on the task). We varied load in the binding condition only, to ensure that the requirement to bind was not confounded with an increase in feature load (see Introduction). It is possible that if intermediate set sizes were manipulated (e.g., 3 objects), binding-specific activity might vary with load in these regions. Further studies are required to establish whether there are also load-dependent processes engaged in VWM binding.

4.2.2 Implications for models of VWM

The focus of our study was to identify whether holding objects in VWM whose features need to be kept bound together requires dedicated resources. We found that processing bindings in VWM engaged regions which overlapped with those involved in encoding single features (see Figure 3A), and additional brain regions. Areas responsible for feature processing therefore appear to support VWM across encoding and maintenance. However, maintaining feature bindings in VWM additionally and specifically recruited parietal regions. This suggests that despite the lack of a behavioral cost to maintain feature bindings in VWM in some studies (Brockmole et al., 2008; Gajewski & Brockmole, 2006; Luck & Vogel, 1997; Vogel et al., 2001) maintaining bound and feature information depends on different representations.

The current data allow us to propose that two levels of representation are active when participants process feature bindings in VWM. One may be a feature-level which runs from encoding through maintenance. The other may be an object-level (i.e., object file, see Treisman (Treisman, 2006) which is specific to maintenance. This level would support those

processes responsible for retaining the link between features once the whole units are no longer in our visual field. This is in line with the assumptions of the Feature Integration Theory (Treisman & Gelade, 1980), with current views on the organization of WM for visual bindings (Baddeley et al., 2011) and also with other fMRI data (Seymour et al., 2008; Xu & Chun, 2007). In a recent revision to their WM model, Baddeley et al. (2011) suggested that different levels of representation, i.e., single features and integrated objects, may be kept simultaneously within the visuo-spatial components of working memory when one processes feature bindings (see Brady et al., 2011 for a similar view). Logie (2011) has argued that the bindings might reflect interactions between cortical systems responsible for retaining individual features. Our fMRI data appear to be consistent with both of these proposals and provide informative data regarding the neural implementation of these different forms of representation, although additional studies will be required to investigate these alternative views.

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Table 1. Clusters showing feature-related activity during VWM encoding. See fMRI analysis strategy, for details of contrasts and post-hoc tests.

Location of peak (x, y, z)	Peak Z	N in cluster	Region	Brodmann area	Post hoc Shp > Col	Post hoc Col > Shp
-26 44 -4	4.66	108	Left middle frontal gyrus	BA11	**	
-50 -58 -14	4.43	332	Left inferior temporal gyrus	BA20	**	
14 -22 4	4.22	259	Thalamus	BA10		**
-52 -4 48	4.14	72	Left precentral gyrus	BA6		**
44 -60 -14	3.79	76	Right fusiform gyrus	BA37	**	
-56 -24 38	3.76	80	Left postcentral gyrus	BA1	**	

** For post-hoc T-tests done at $p < .001$; Shp = shape and Col = Color

Table 2. Clusters showing above-threshold binding-specific activity during VWM maintenance. See fMRI analysis strategy, for details of contrasts (see also Supplementary Figure 2).

Binding maintenance						
Location of peak (x, y, z)	Peak Z	N in cluster	Region	Brodmann area		
-44 -64 -14	5.22	227	Left fusiform gyrus	BA37		
-40 -34 62	4.57	108	Left postcentral gyrus	BA2		
<i>Including subpeak:</i>						
-26 -50 64	4.04		Left superior parietal lobule	BA7		
-30 -10 44	4.44	251	Left dorsal premotor cortex/ middle frontal gyrus	BA6		
-42 -28 32	4.43	322	Left inferior parietal lobule	BA40/2		
<i>Including subpeak:</i>						
-40 -48 30	4.29		Left inferior parietal lobule	BA40		
					Post hoc	Post hoc
Feature maintenance					Shp > Col	Col > Shp
-38 18 -4	4.24	212	Left inferior frontal gyrus	BA47		**
4 12 40	3.79	83	Anterior cingulate gyrus	BA32		**

** For post-hoc *T*-contrasts at $P < .001$; B2 = Binding 2 items and B4 = Binding 4 items; Shp = shape and Col = Color

Figure captions

Figure 1. Task design and an example trial for each of the conditions of the VWM binding task. Conditions assessing VWM for single features presented 4 items. Shape-color binding was assessed in two separate conditions, one presenting 4 items and the other one presenting 2 items. The rationale for this manipulation is described in the Methods.

Figure 2. Mean proportion of correct recognition for each condition of the VWM binding task (chance level is 50%). Error bars represent the standard errors of the mean. For details of the different conditions see Methods and Figure 1. For details of measures see Results.

Figure 3. Sections (A) illustrate feature-related encoding phase activity (red) and binding-specific maintenance phase activity (green), in bilateral fusiform gyrus (R-Fus and L-Fus; left panel), in fusiform gyrus and left parietal cortex (L-IPL; right panel). Significant clusters are overlaid on the smoothed group-averaged structural scan. Parameter estimate plots (B) show encoding (left panel) and maintenance phase activity (right panel) in L-Fus at the peak of the cluster in which feature-related encoding phase activity (left panel) overlapped with binding-specific maintenance phase activity (right panel). Plots show mean parameter estimates (arbitrary units) and error bars represent the standard error of the mean.

Supplementary Material

Regions of Interest (ROIs) analysis

In addition to the whole-brain analysis, binding-specific activity was also assessed in a set of regions of interest (ROIs) defined *a priori*. From the literature, we identified studies assessing activity associated with the binding of feature conjunctions in VWM tasks (Piekema et al., 2006; Shafritz et al., 2002; Song & Jiang, 2006; Staresina & Davachi, 2010; Todd & Marois, 2004; Xu, 2007). These studies, contrasts and the co-ordinates of significant peaks of activity are listed in the table below. We chose areas which had been previously found to be activated by tasks involving binding objects or colors to spatial location (Piekema et al., 2006; Todd & Marois, 2004; see also Mitchell, Johnson, Raye, & D'Esposito, 2000; Piekema, Kessels, Rijpkema, & Fernandez, 2009; Piekema et al., 2010) or binding object parts into unified representations (Shafritz et al., 2002; Song & Jiang, 2006; Staresina & Davachi, 2010; Xu, 2007). The cortical ROIs were defined as spheres of radius = 5 mm³ from the voxel location closest to the *a priori* coordinates; the radius for the Medial Temporal Lobe (MTL) ROI was 3 mm³. Each ROI analysis was thresholded using a small-volume FWE correction (see Methods).

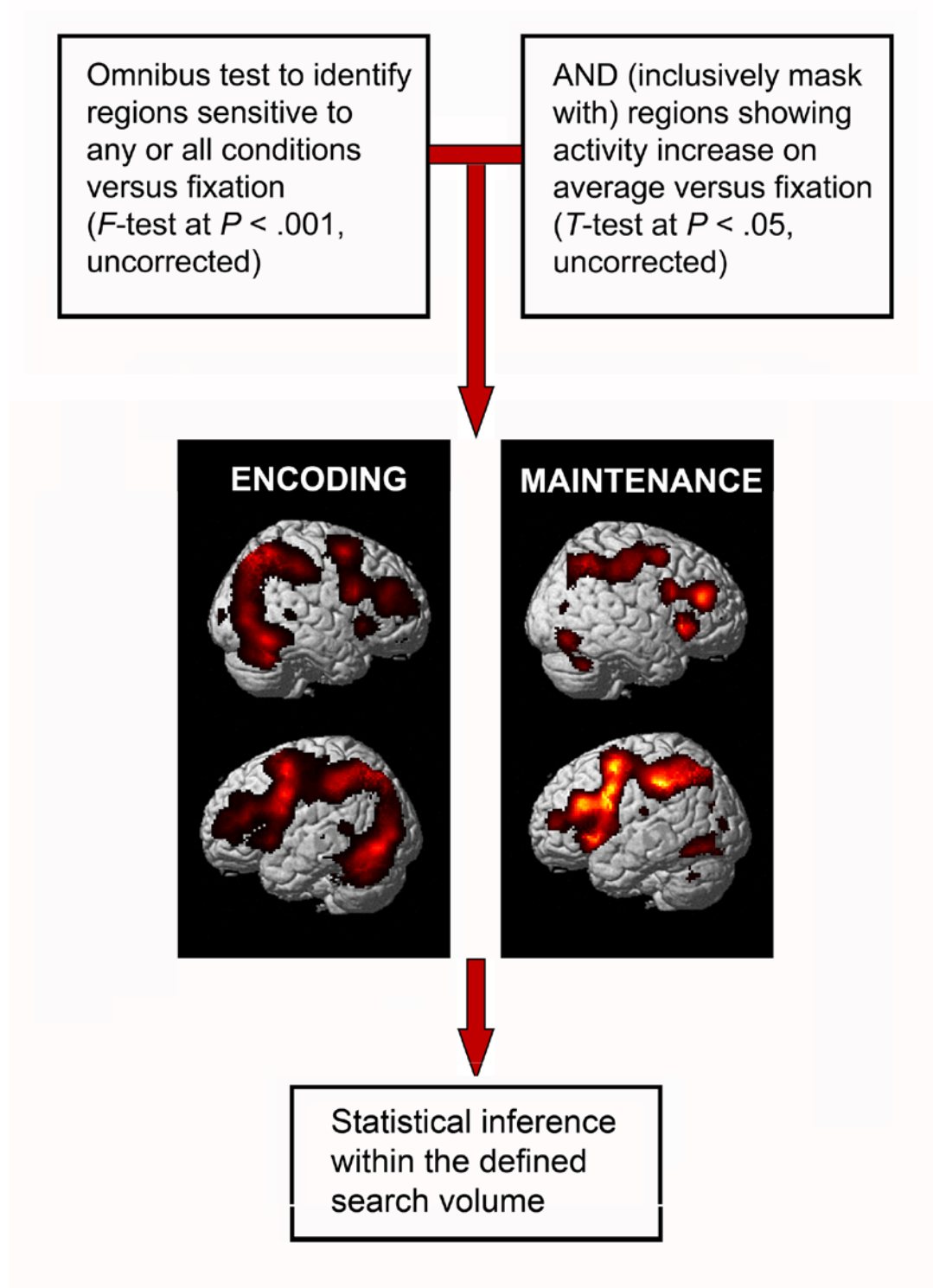
The *a priori* ROI analyses for the encoding phase revealed significantly greater activity for binding than feature conditions in the right lateral occipital complex (see Table 1). No other ROIs analyzed during this phase showed suprathreshold activity. For the maintenance phase, significant activation was observed in the left lateral occipital complex and frontal eye. No other ROIs, including those in the MTL, showed suprathreshold activity. Possible interpretations and implications of these findings are briefly discussed in the manuscript.

Supplementary Table 1. Details of ROI analyses of binding-specific activity. *A priori* coordinates derived from previous findings of activations during VWM binding tasks are listed. Region descriptions as well as Talairach coordinates are those of the original authors. The results of the current ROI analyses are given for encoding and maintenance trial phases: “ns” indicates a non-significant finding. The number of suprathreshold voxels within the region is given. For details of the analysis methods see Methods and Results: Analysis Strategy.

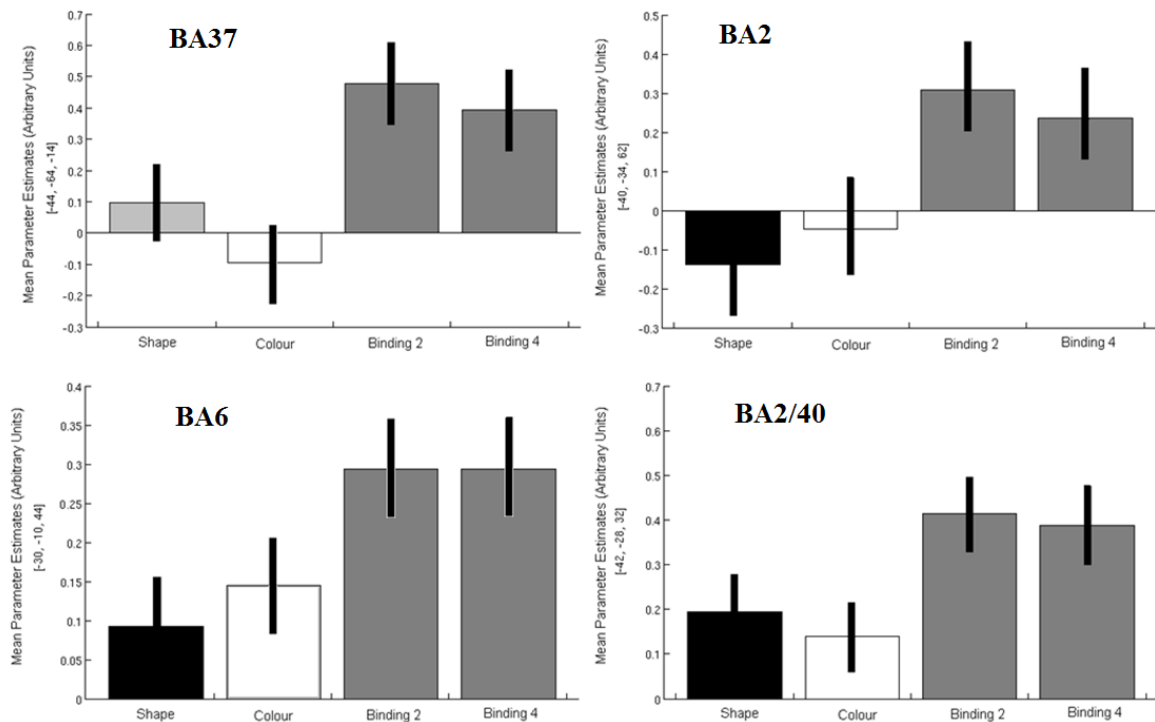
Previous findings				Current Study	
Authors	ROIs	x,y,z	Contrasts	Encoding (N voxels)	Maintenance (N voxels)
(Shafritz et al., 2002)	Intra-parietal cortex BA 7	[40 -39 47]	Binding > Features	ns	ns
	Superior parietal cortex BA 7	[16 -58 56]		ns	ns
(Xu, 2007b)	Intra-parietal sulcus	R [23 -59 45]	Binding > Feature	ns	ns
(Todd & Marois, 2004)	BA 7	L [-22 -65 42]	Sensitivity to VWM capacity	ns	ns
(Song & Jiang, 2006)	Superior parietal lobule BA 7	R [30 -60 48] L [-24 -60 48]	(Shape = Binding) >Color	ns	ns
			Sensitivity to VWM load	ns	ns
	Lateral occipital cortex (fusiform gyrus) BA 37	R [45 -63 -15] L [-48 -60 -21]	(Shape = Binding) >Color	13 ns	ns 3
	Frontal eye field BA 6/8	R [30 -12 51] L [-27 -9 48]	Shape > (Binding = Color).	ns ns	ns 66
	Inferior frontal sulcus BA 44	R [39 -3 33] L [-45 0 30]		ns ns	ns ns
	Supplementary motor area BA 6	[12 9 51]	Sensitivity to VWM load	ns	ns
(Piekema et al., 2006)	Hippocampus	R [30 -20 -10]	Delay related activity for relational binding (i.e., item-location associations)	ns	Ns
(Staresina & Davachi,	Perirhinal cortex	R [28 -14 -28]	Memory: Objects missed, Objects	ns	Ns

2010)		L [-24 -15 -30]	correctly remembered and Object-Color	ns	ns
	Entorhinal cortex	R [20 -8 -24]	combinations remembered.	ns	ns
		L [-20 -6 -24]	Fragmentation: whole object, objects in two fragments, and objects in four fragments. No Memory x Fragmentation interaction in the perirhinal cortex.	ns	ns

An FWE-corrected threshold was applied within each ROI at $P < 0.05$, using the small-volume correction within SPM8.



Supplementary Figure 1. Schematic showing the masking procedure used to define the analysis search volumes for encoding and maintenance phases (see 3.2, fMRI data analysis strategy).



Supplementary Figure 2. Results of additional analysis of binding-specific activity during VWM maintenance in which regions showing differential activity in the binding conditions according to set size were not discounted. The parameter estimate plots show activity in each condition relative to fixation. They show that holding two or four bindings in VWM led to similar activation in the four key regions which showed binding specific activity. The table at the bottom lists the regions showing suprathreshold activity during this supplementary analysis. It is worth noting that the differences between these regions and those presented in Table 1 of the manuscript are only in the size of the clusters which were slightly bigger in this new analysis.

Location of peak (x, y, z)	Peak Z	N in cluster	Region	Brodmann area
-44 -64 -14	5.22	242	Left fusiform gyrus	BA37
-40 -34 62	4.57	125	Left postcentral gyrus	BA2
-30 -10 44	4.44	329	Left middle frontal gyrus	BA6
-42 -28 32	4.43	348	Left inferior parietal lobule	BA2/40